Assessing the relative importance of isolated Ficus trees to insectivorous birds in an Indian human-modified tropical landscape

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Compliance with ethical standards

This research was conducted with ethical approval from the University of Oxford (Departmental CUREC reference number: SOGE C1A-99). Surveys were conducted with permission from local landowners where necessary, and permission to conduct this field work in India was granted by the High Commission of India, London, under visa number 4246496. Field studies did not impact the welfare of the animals studied, and the authors have no conflicts of interest to declare.

Abstract

The destruction of forest for agricultural expansion has created a vast estate of human-modified land in tropical regions. One group of organisms that are particularly vulnerable to the loss of forest habitat are insectivorous birds. Despite this, few conservation strategies have been identified for this group in human-modified landscapes. We survey the use of 104 isolated trees by insectivorous birds in rural Assam, India. We used an information theoretic model comparison approach to determine the important variables driving insectivorous bird diversity within these isolated trees. Our work demonstrates that the conservation of large trees in human-modified landscapes may play an important role in maintaining bird diversity and ecological function beyond the forest edge. More specifically, we found that isolated *Ficus* trees hold assemblages with particularly high insectivore abundance, richness and functional diversity when compared to other isolated fruit and large trees. We argue that, where present, *Ficus* trees should be actively conserved in human-modified landscapes to maintain the composition of insectivore communities in a "*Ficus* first" strategy.

Keywords Conservation beyond protected areas, birds, ecological function, *Ficus*, India, insectivores, isolated trees, multimodel inference

Introduction

As agricultural expansion continues to fragment the world's tropical forests and occupy large areas of land (Phalan et al. 2013), it is increasingly important to devise conservation strategies for human-modified landscapes (Chazdon et al. 2009; Gardner et al. 2009; Melo et al. 2013). The conversion of forest has a range of impacts on different taxa. Here our focus is on the largest avian feeding guild, insectivorous

65 birds, an ecological group that is considered particularly vulnerable to habitat loss
66 (Tscharntke et al. 2008).

67 Several studies have demonstrated lower abundance and species richness of
68 insectivores in human-modified landscapes compared to intact forest habitats (Harvey
69 et al. 2006; Şekercioğlu 2012). Studies in habitat fragments have found similar
70 results; especially when there is limited tree cover surrounding fragments (Stouffer
71 and Bierregaard 1995). Not only does this cause deterioration in the conservation
72 status of insectivorous birds (Şekercioğlu et al. 2002), but it also diminishes their
73 beneficial pest control services (Van Bael et al. 2008; Karp and Daily 2013).

74 One possible strategy to mitigate the decline of insectivorous birds in human-
75 modified landscapes might be the conservation of isolated trees (Manning et al. 2006;
76 Cottee-Jones et al. 2015a). These trees can increase the abundance and richness of
77 insectivores by providing connectivity between forest remnants for forest-dependent
78 species (Harvey et al. 2006), along with feeding and nesting sites for matrix-tolerant
79 taxa (Şekercioğlu et al. 2007), thereby moderating the impact of habitat loss
80 (Şekercioğlu 2012). However, our understanding of conservation tools that are
81 appropriate in human-modified landscapes represents a critical frontier in tropical
82 conservation biology (Tscharntke et al. 2008; Melo et al. 2013). Indeed, we have very
83 limited experimental evidence to help guide conservation practitioners working in the
84 2.5 billion ha of tropical land area that has been modified by humans (see Supporting
85 Information 1; Fischer et al. 2006; Melo et al. 2013).

86 *Ficus* trees have long been recognised as important food resources for frugivores
87 (Terborgh 1986; Cottee-Jones et al. 2015b), with almost 1,000 frugivorous bird
88 species recorded consuming *Ficus* fruit (Shanahan et al. 2001). They may also be
89 overlooked but important foraging sites for insectivores. Their co-evolved mutualism

with pollinating fig wasps (Hymenoptera, Agaonidae, Agaoninae) means that millions of fig wasps (and non-pollinating fig wasps; Hymenoptera, Chalcidoidea) are found in association with fruiting figs (Harrison 2003; Bain et al. 2013). As well as being a food resource for insectivorous birds themselves, these fig wasps are also the prey of other invertebrates that inhabit or visit *Ficus* trees (Schatz et al. 2008). Numerous other insects, including heteropterans, nematodes, coleopterans, and fruit flies, also exploit the extremely large fruit crop, which may number as many as one million syconia per tree (Cushman et al. 1998). Indeed, notwithstanding chronic under-sampling, there are published records of 1,875 species of arthropod feeding on *Ficus*, including 742 species feeding on syconia, 481 feeding on sap, 369 leaf-chewers, and 283 wood borers (Basset et al. 1997). Ants (Hymenoptera: Formicidae) for example, have been found to specialise in predating non-pollinating fig wasps in some dioceous *Ficus* species, predate on fig dwelling herbivorous insects, consume partially eaten ripe syconia, and nest in figs (Schatz et al. 2008; Harrison 2013). The complex trunk morphology of many strangler *Ficus* trees provides further habitat for arthropods, all of which suggests that *Ficus* trees may be attractive feeding sites for insectivorous birds.

In this study, we sought to test whether isolated *Ficus* trees were particularly important foraging sites for insectivorous birds in human-modified landscapes, relative to other fruit-bearing and large non-fruit trees found in open habitats, as indicated by higher levels of insectivore richness, abundance, and functional diversity.

Materials and methods

Study area

The study took place from April 2012 to June 2013 in the Golaghat District of Assam, North-east India (see Fig. 1). The study site is a ≈250 km^2 area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. The elevation of the study area ranges between 30 and 100 m above sea level, and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in the June to September monsoon (Shrivastava and Heinen 2007). The annual temperature range varies from an average minimum of 5°C to an average maximum of 35°C (Barua and Sharma 1999).

The original habitat of moist subtropical deciduous forest (Champion and Seth 1968) was largely cleared following the local commercialisation of tea production in 1840 (Shrivastava and Heinen 2007). Remnants of the original forest remain in the 7.65 km^2 Panbari Forest Reserve on the edge of the Karbi Hills, and in the 430 km^2 Kaziranga National Park (Barua and Sharma 1999). Other small areas of forest regrowth exist, but are typically less than 1 ha. Agriculture is the dominant land-use, with a mixture of small-holder rice cultivation, village home gardens, and large commercial tea estates.

Focal tree sampling

To compare the insectivore assemblages visiting *Ficus* trees to other isolated trees in this human-modified landscape, we surveyed three categories of focal tree: 1) isolated *Ficus* trees, which we surveyed when in fruit; 2) isolated fruit trees that did not belong to the *Ficus* genus, which we surveyed when in fruit; 3) isolated large, non-fruiting trees (i.e. trees that did not produce fruit during the study). We surveyed a total of 40 *Ficus* trees, 33 fruit trees, and 31 large non-fruiting trees in the study area (Table 1). The selection of focal *Ficus* and other non-*Ficus* fruit trees (herein in "fruit

trees") was determined by their fruiting cycle; only trees with crops of ripe fruit were surveyed. Large non-fruiting trees ("large trees") were selected from the largest trees in the landscape, exclusive of the two previous groups, with a minimum circumference at breast height of over 1 m, so that we had a dataset that was comparable in tree stature to the *Ficus* trees.

For each tree, we measured the diameter at breast height (DBH), estimated the maximum tree height with a clinometer, and estimated the canopy area by measuring the canopy diameter at ground level along two axes, deriving canopy area using the formula for an ellipse. To obtain a single estimate for tree size, a Principal Components Analysis (PCA) with Kaiser stopping criterion extraction (eigenvalues >1) and oblique rotation was conducted using DBH, maximum height, and canopy area in IBM SPSS Statistics 22 (IBM 2013). The first axis of this PCA explained over 80% of the variance in the three variables and was significantly correlated with all three tree size variables (Pearson's product-moment correlation coefficient greater than 0.8 in each case). Thus, the first axis was used as our tree size variable. The intensity of human land-use within a 100 m radius of each focal tree was recorded using a three-point scale (where 0 is very little human land use; 1 is some human land use, such as cultivation; and 2 is intense human land use, in cases where a road, house, or paddy field were present).

We measured the distance to the nearest protected area with intact forest by marking the focal trees with a GPSmap 62s device, and then overlaying the GPS markers on Landsat 8 satellite images of the region in ArcGIS 10.2.1 (ESRI 2014). We digitised the protected area borders through an on-screen visual interpretation, and then measured the distance (in km) of each focal tree to the nearest protected area. In all cases, protected areas held the only high-quality forest habitat left in the study

landscape. In addition to protected areas, small (≤1 ha), low-quality wooded areas were located through consultation with local landholders and marked with a GPS device. We then recorded a second distance measurement: the distance to the nearest wooded area of any quality (whether a protected area or small wooded area).

Insectivore surveys

Each focal tree was surveyed once, for three hours, from first light. Surveys were only conducted in fair weather conditions. During the survey, a single observer would watch the tree from a concealed position with a good view, typically about 20 m from the trunk. Each individual bird that landed in the tree was recorded, and birds that made repeated visits to and from the tree were denoted with an asterisk to avoid double counting. Trees in the *Ficus* and fruit categories were only surveyed when the crop was ripe. Deforestation in the study area occurred over 150 years ago, and was largely uniform in timing, so differential rates of matrix assemblage relaxation were not considered to have an effect on bird communities in the study area. As all trees were surveyed in the same Assamese season, the presence or absence of migratory species was consistent across the three tree groups.

Each species was classified into primary dietary guilds (frugivore, nectivore, insectivore, granivore, or carnivore; omnivores were classified according to their main food type, and were not included in any further analyses on insectivorous birds as they may have been attracted to *Ficus* and fruit trees by the fruit present) following del Hoyo et al. (1992–2002; 2003–2011). Nomenclature also followed del Hoyo et al. (1992–2002; 2003–2011).

Ecomorphological data collection

186 To calculate functional diversity scores, we preferred to use ecomorphological trait
187 data from the insectivores recorded in the surveys rather than guild classifications
188 extracted from the literature or assessed using our field experience. This is because
189 continuous traits have been argued to produce more accurate representations of
190 species' functional roles in ecosystems (McGill et al. 2006), and the use of continuous
191 trait data removes the need to arbitrarily assign species into different categories. We
192 defined a "trait" as a measurable aspect of an organism, which determines its
193 interaction with the environment (Flynn et al. 2009). Here we were interested in the
194 foraging and dispersal capacity of insectivorous birds, so we measured traits
195 associated with locomotive behaviour, dispersal ability, gape size, bill structure, and
196 body size (Derryberry et al. 2011; Claramunt et al. 2012). In order to obtain
197 ecomorphological trait data, each species recorded in the surveys was measured
198 following Edward Grey Institute protocols at the British Natural History Museum's
199 ornithological collections (Supporting information 2).

200 *Functional diversity calculation*

201 We follow the definition of functional diversity as the distribution of functional traits
202 within multidimensional niche space (Petchey and Gaston 2006), and used Laliberté
203 and Legendre's functional dispersion (FDis) index to measure functional diversity in
204 our dataset (Laliberté and Legendre 2010; please see Supporting information 3 for a
205 justification of the method selected). We calculated FDis for each of our focal trees
206 using "package FD" in Programme R (Laliberté and Shipley 2013; R Core Team
207 2014).

208 As our trait data were measured on a continuous scale, rather than classified into
209 nominal groups, a species–species uncorrected distance matrix was computed. A
210 Principal Co-ordinates Analysis (PCoA) was performed after the distance matrix was

corrected for negative eigenvalues. Each trait axis was standardised to have a mean of zero and a standard deviation of one (Petchey and Gaston 2006). These corrected PCoA trait axes were used to calculate the FDis scores for our focal trees. FDis could not be computed for trees with no insectivore records, but these trees were included in further analyses with index scores of 0. Similarly, trees with only one species of insectivore were given a score of 0 following Laliberté and Shipley (2013). We checked the functional relationships between the sampled insectivorous bird species by constructing a dendrogram: we transformed the species–trait data into a distance matrix (Euclidean distance), and applied the UPGMA clustering algorithm. The resulting dendrogram was subsequently converted into a tree object and plotted (Fig. 2).

Statistical analysis

The effect of tree size, land-use intensity, distance to the nearest protected area and nearest forest of any type, and tree type on insectivore abundance, richness, and FDis (the three response variables) were examined using an information-theoretic approach (Burnham and Anderson 2002). For each response variable, we fitted a full generalized linear model (GLM), i.e. a model with all predictor variables included. Abundance and richness are count data and thus for these response variables we used GLMs with the Poisson family and a log link function. As the Poisson distribution assumes that the mean is equal to the variance, a quasi-Poisson model was fitted with each response variable to assess for over-dispersion. In both cases, the data were found to be over-dispersed and thus quasi-AIC_c ($QAIC_c$; Richards 2008; Bolker 2016) was used for subsequent model comparisons using models with these two response variables. Functional diversity was found to be normally distributed following a log transformation; as the logarithm of zero is not defined, a constant of 0.1 was added to

all FDis values. Thus, for models in which FDis was used as the response variable, we fitted GLMs with the Gaussian family and identity link function.

Multicollinearity between the continuous predictor variables was assessed using variance inflation factors using the 'car' R package (Fox and Weisberg 2011) and a threshold of five. All continuous predictors had variance inflation factors of less than five and so were included in the model comparisons. Outliers were assessed using Cook's distance and a threshold of one. Two data points were removed prior to the model comparisons based on this criterion. Continuous predictors were assessed for normality: tree size and both distance measures were log transformed to induce normality. A constant of 1.5 was added to tree size values as the raw values (PCA axis values) contained negative numbers.

Model comparison was undertaken using an information theoretic approach. When FDis was used as the response variable, we fitted a complete set of models considering all predictor variables using the dredge function in the MuMIn R package (Bartoń 2016). Models were ranked according to AIC_c values (Burnham and Anderson 2002) and we also recorded the ΔAIC_c values and the AIC_c weights for each model.

As the dispersion parameter in the Poisson GLM is taken to be one, and model fits using abundance and richness were found to be over-dispersed, we compared models with these two response variables using the quasi-Poisson family and $QAIC_c$ (Richards 2008). Thus, instead of using maximum likelihood estimation, we focused on maximising the "quasi-likelihood." For each set of model comparisons, we extracted the dispersion parameter from the full model (i.e. with all predictors) using functions provided by Bolker (2016). We then, separately for each response variable (i.e. abundance and richness), fitted a full set of models considering all predictors and

compared models based on their $QAIC_c$ values; again, also storing the $\Delta QAIC_c$ values and the $QAIC_c$ weights. Thus, in total we had three model comparison tables, one for each of the three response variables.

To evaluate the importance of individual variables, for each model comparison table separately we calculated the weight of evidence (WoE) of each predictor by summing the AIC_c weights (or $QAIC_c$ weights) for each model in which a predictor variable was included (Burnham and Anderson 2002; see also Giam and Olden 2016). As the AIC_c and $QAIC_c$ weights sum to one for a given model comparison, the WoE values are constrained to be between 0 and 1. However, WoE values are not expected to be zero even in cases where a predictor variable has no predictive value (see Burnham and Anderson 2002, p. 345). Thus, we followed Burnham and Anderson (2002, p. 345 onwards) and used a bootstrap methodology to compute a baseline WoE value for each predictor variable in each model comparison table. This worked by creating an algorithm that took the i^{th} predictor and randomised the values whilst holding the values of the other predictor variables constant. The model comparison was then repeated and the WoE values calculated in the standard manner. The algorithm then re-arranged the values in the i^{th} predictor back to their original order and moved onto the $i+1^{th}$ predictor, and so on, until all predictor variables had been randomised. This process was then repeated 500 times and the median value (the bootstrap distribution of WoE values is occasionally skewed and thus the median is a preferable metric; Burnham and Anderson 2002) taken. This approach was only undertaken for the model comparison using FDis as the response variable, as it is straightforward to implement in the context of Gaussian GLMs. In the model comparisons using abundance and richness as the response variables, the models were fitted using the Poisson/quasi-Poisson families and it was found that randomising the predictor values

frequently resulted in very high degrees of over-dispersion and the failure of models to converge. Based on the bootstrap WoE results using FDis, we tentatively used a baseline of 0.3 when analysing WoE results from model comparisons using abundance and richness.

For each model comparison table, we took the full model and best model (i.e. lowest AIC_c or $QAIC_c$ value) and examined the residual plots (e.g. residuals against fitted values, standardised residual values etc.) for any patterns. We also tested for spatial autocorrelation in the residuals of the best model fits using the 'spdep' R package (Bivand and Paris 2015), the nb2listw function and row standardised weights. When FDis was used as the response variable, examination of the residuals revealed some sort of pattern; potentially indicating that a variable was missing from the model (Zuur et al. 2009). To account for this, we re-ran the model selection whilst including an interaction term between tree size and tree type in the full model. This resulted in a much more normal distribution of residuals in the best model fit. As such, we re-ran the FDis model selection using the interaction as a fixed term within the 'dredge' function in MuMIn. As the interaction term is fixed, it means that the individual variables 'tree size' and 'tree type' are also fixed. We also re-ran the abundance and richness model selection analyses with this interaction term to assess whether the interaction was important in regards to these response variables. As it was found to improve the distributions of errors in the abundance and richness models, we also fixed the interaction term in this model selection. Finally, for the FDis model comparison we looked at the R^2 value of the best model, whilst for the abundance and richness model comparisons we computed pseudo R^2 values for the best models using the formula: 1 - (model deviance / null deviance).

Results

311 Over the 104 surveys, 33 species of insectivorous bird were recorded. The most
312 frequently recorded species were the Oriental white-eye (*Zosterops palpebrosus*) with
313 55 records, common tailorbird (*Orthotomus sutorius*) with 54, and the Oriental
314 magpie robin (*Copsychus saularis*) with 53. The Oriental white-eye was also the most
315 abundant species, with 146 individual records, followed by the great tit (*Parus major*)
316 with 86, and the Oriental magpie robin with 84.

317 *Ficus* trees had higher mean abundance (12.0, standard error = 0.96), richness (7.0,
318 SE = 0.38) and FDis (1.3, SE = 0.07) values compared to the other tree categories,
319 followed by large non-fruit trees (mean richness = 3.7, 2.5 and 0.8, respectively; SE =
320 0.74, 0.45 and 0.15) and then non-*Ficus* fruit trees (2.7, 1.9 and 0.6, SE = 0.37, 0.23
321 and 0.11; Fig. 3).

322 The results of the multimodel comparison analyses are described below for each of
323 the three response variables in turn.

324 *Abundance*

325 The inclusion of the interaction term resulted in a more normal distribution of errors
326 in the full and best models (for both the abundance and richness models), although
327 there was still a degree of spread towards the extreme tails of the distribution;
328 however, it is known that residuals in Poisson regression models are only
329 approximately normal, and there is expected to be a degree of spread towards the
330 extreme tails of the distribution. Thus, the model selections based on both the
331 abundance and richness (results presented below) response variables were run with
332 the interaction term included. When abundance was used as the response variable,
333 there was one model within 2 $\Delta QAIC_c$ values of the best model. The best model
334 contained tree size, tree type and the interaction between them (i.e. the fixed

parameters in the model selection) and the distance to the nearest protected area with intact forest (Table 2a), and had a pseudo-R^2 value of 0.62. The distance to a protected area variable also had a relatively high WoE value (0.59), which was larger than the baseline of 0.3 that we employed for the quasi-Poisson model selections in this study. The parameter estimates for the best model (using the quasi-Poisson family) are included in Table S1 in Supporting information 4. Using the quasi-Poisson family results in the same parameter estimates as the standard Poisson family. We did not look at the significance of parameter estimates for the best model (including for the best richness and FDis models, below), as this is not advised within information theoretic model comparison approaches (Burnham and Anderson 2002). There was no significant spatial autocorrelation in the residuals of the best model (Moran's I = 0.03; P = 0.31). In regards to the tree type variable, the parameter estimates were negative and relatively large (Table S1) and thus indicated that both fruit trees and large non-fruiting trees supported lower abundance than *Ficus* trees. The effect of tree size was positive, indicating abundance increased with the size of tree. Consideration of the interaction term parameter estimates (Table S1) indicates that this is primarily driven by the large non-fruiting tree category, i.e. the slope between abundance and tree size is steeper for this tree category relative to the other two. Interestingly, the effect of distance was positive, which implies that the abundance of insectivorous birds increased with distance to the nearest protected area with intact forest. The WoE values for the other distance variable and land use were both below the baseline value (Table 2a), and thus these variables can be considered relatively unimportant in determining abundance in this system.

Richness

When richness was used as the response variable, there were two models within 2 $\Delta QAIC_c$ values of the best model. The best model contained tree size, tree type and the interaction between them (i.e. the fixed parameters in the model selection) (Table 2b), and had a pseudo-R^2 value of 0.60. The parameter estimates for the best model (using the quasi-Poisson family) are included in Table S2 in Supporting information 4. In regards to the tree type variable, the parameter estimates were again negative and relatively large (Table S2) and thus indicated that both fruit trees and large non-fruiting trees supported lower richness than *Ficus* trees. As with the best model using abundance, the effect of tree size was positive and the interaction term parameter estimates (Table S2) indicate that this effect is primarily driven by the large non-fruiting tree category. Whilst land use and the distance to the nearest protected area with intact forest were included in the models within 2 $\Delta QAIC_c$ of the best model, both variables had WoE values below the baseline of 0.3. The second distance variable also had a WoE value below 0.3 (Table 2b). There was no significant spatial autocorrelation in the residuals of the best model (Moran's I = 0.03; $P = 0.29$).

Functional Dispersion

When FDis was used as a response variable the best model had an adjusted R^2 value of 0.29 (see Table S3 in Supporting information 4 for parameter estimates). There were no additional models within 2 ΔAIC_c values of the best model (Table 3). As described above, the FDis model selection analyses included an interaction term between tree size and tree type as a fixed term in the model selection, to ensure a more normal distribution of errors. Thus, tree type, tree size and the interaction term were all included in the best model by default and the WoE values for these variables are not interpretable (see Table S3). In regards to the tree type variable, the parameter estimates were negative and relatively large (Table S3) and thus indicated that both

fruit trees and large non-fruiting trees supported lower FDis than *Ficus* trees. The effect of tree size in the best model was small (-0.06) and negative, indicating that FDis actually decreased with increasing tree size. However, closer inspection of the best model's parameter estimates indicated that this was probably driven by the interaction between tree type and tree size; the slope of the FDis – tree size relationship was steeper for both fruit trees and large non-fruiting trees relative to *Ficus* trees. Land use was also included in the best model and had a relatively high WoE value, which was considerably larger than the bootstrapped baseline value. Inspection of the best model's parameter estimates indicated that increasing land use intensity resulted in a decrease in FDis. Neither of the distance variables were included in the best model, and both had WoE values lower than the baseline values (Table 3). There was no significant spatial autocorrelation in the residuals of the best model (Moran's I = -0.02; $P = 0.46$).

Discussion

The conversion of tropical forest to agricultural production causes changes in insectivorous species composition and functional diversity (Tscharntke et al. 2008; Azhar et al. 2013; Edwards et al. 2013). However, we found that isolated *Ficus* trees provide important micro-site level habitat for insectivores in the human-modified Assamese landscape. Compared to the other tree categories, *Ficus* trees had consistently higher insectivore richness, abundance and functional diversity, suggesting that these trees may be more valuable from a conservation perspective in these modified landscapes than other isolated trees.

In addition to tree type, our model comparisons also indicated that tree size and the interaction between tree size and tree type were important variables. Although these variables were fixed in the model comparisons, the fact that they were needed to be fixed to improve the error distribution indicates that they are important. In addition, exploratory analysis indicated, once the assumptions of GLMs were temporarily relaxed, that even when the model comparisons were run without fixing these variables they consistently had high WoE values and were included in the best models (results not shown). The interaction terms in the best models indicated that each of the slopes between abundance, richness and FDis, and tree size were steeper in the large non-fruit tree category relative to the other two categories. Figure 4 illustrates these relationships for richness using scaled size (i.e. re-scaling each tree size such that the data cover the same range for each tree type) for each of the three tree types. It can be seen that for *Ficus* trees and the large non-fruit trees category, species richness generally increases with tree size; although the relationship appears to flatten out at large sizes for *Ficus* and the relationship is thus steeper for the large non-fruit tree category. However, there does not appear to be any relationship between tree size and richness for non-*Ficus* fruit trees. It should also be noted that if the tree sizes are simply standardised by the largest tree in the dataset (i.e. not accounting for tree type) the *Ficus* line still lies above the other two lines in Fig. 4 and thus, whilst the relationship is steeper for large non-fruit trees, for any given tree size there is a higher species richness in *Ficus* trees relative to the other tree types. The fact that the relationship is steeper for large non-fruit trees relative to *Ficus* trees is likely due in part to the fact the *Ficus* trees are generally larger than trees in the other two categories and thus are there are fewer small *Ficus* trees in our dataset, and in tropical landscapes more generally (partly due to the “strangler” life history of many species).

Nonetheless, in regards to conservation actions and assuming that the retention of ecological services such as pest control is a priority (and assuming that the birds recorded in isolated trees are also foraging in agricultural crops), the conservation of large trees *per se* may be the most effective strategy. In this case, isolated *Ficus* trees would again be a conservation priority, as they were generally the largest trees in the study area.

When abundance was used as the response variable, the model comparison results indicated that abundance increased with increasing distance from a protected area with intact forest. This is an interesting and counter-intuitive finding and is possibly due to the effect of matrix specialist birds (Şekercioğlu 2012). Some of the species with the highest number of recorded individuals were matrix specialist species, such as great tit (*Parus major)*, common iora *(Aegithina tiphia*), and crimson sunbird (*Aethopyga siparaja)*. These birds showed a distinct preference for non-forest habitats, with increasing occurrence as the distance from the forest increased.

Interestingly, the effect of land use was only important in the model comparisons based on FDis. It was found that increasing land use intensity resulted in a decrease in FDis. This is to be expected and several previous studies have shown that land use change and intensification lead to a reduction in functional diversity (e.g. Schweiger et al. 2007; Flynn et al. 2009; Laliberté et al. 2010). The reason why land use was not an important variable in the abundance and richness model comparisons is unknown. However, again, it may be due to the presence of matrix specialists in the landscape. The inclusion of matrix specialist bird species in analyses such as those in this study have sometimes been found to mask the effects of land use change on abundance and richness (Matthews et al. 2014). If these matrix specialist species are relatively immune to land use change and increase in abundance and richness in more disturbed

environments, but also possess similar trait values to one another, they may compensate the loss of forest specialist abundance and richness with increasing land use intensity whilst simultaneously resulting in a reduction in FDis, as we observed. It is also possible that our coarse three-level ordinal land use scale did not contain enough information to uncover relationships between abundance and richness, and land use.

Several studies have argued for the need to conserve isolated trees in human-modified habitat (Manning et al. 2006; Şekercioğlu et al. 2007; Fischer et al. 2010). Our results build upon these arguments, adding that isolated trees can be important resources for insectivores as well as frugivores (Luck and Daily 2003), and tree-hole nesters (Manning et al. 2004). We consider this a valuable finding, as there are few conservation strategies focused on this vulnerable group in modified landscapes. We also add that *Ficus* trees may be particularly important for insectivorous birds in human-modified landscapes. In our study area at least, this implies that conserving *Ficus* trees ahead of other tree types may be a more effective conservation strategy than conserving isolated trees at random. If *Ficus* trees are found to be similarly important to insectivorous birds in modified landscapes on a wider spatial scale, a "*Ficus* first" approach to isolated tree conservation may be effective across the tropics (see Cottee-Jones & Whittaker 2015; Cottee-Jones et al. 2016). Although additional studies on *Ficus* trees and insectivores are lacking, *Ficus* have been found to support rich and abundant insect communities wherever they have been studied (Basset and Novotny 1999; Pereira et al. 2000; Bain et al. 2013).

The conservation of isolated trees in modified landscapes presents significant challenges, however. It requires a long-term vision with extensive commitment from landowners (Manning et al. 2004), and can incur substantial costs if natural

regeneration is insufficient (Fischer et al. 2010). The regeneration of *Ficus* trees may be particularly challenging, as many species are epiphytic in their early life stages, and so depend upon the presence of large host trees (Leighton and Leighton 1983). Fortunately, evidence from the study area indicates that, in this region at least, *Ficus* trees are regenerating faster in modified habitats than are isolated trees in other parts of the world (Gibbons et al. 2008; Cottee-Jones et al. 2016). If the conservation of isolated *Ficus* trees was adopted in legislation, there is scope for future work to focus on thresholds for the tree size required to qualify for protection, and the size of buffer zones around isolated trees where land-use practices may be restricted.

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Tables

Table 1: Characteristics of the three isolated tree groups surveyed in Assam, India. DBH is diameter at breast height. Values for DBH, height, and canopy area are mean ± standard error. The five most surveyed species are listed in order of decreasing number of surveys. Fruit refers to large fruit-trees other than *Ficus* and Large to the category of large trees that did not bear fruit during the study.

Characteristic	*Ficus*	Fruit	Large
Total no. of individuals surveyed	40	33	31
Total no. of species surveyed	6	12	15
DBH (m)	1.51±0.13	0.45±0.02	0.61±0.05
Height (m)	27.29±1.40	18.86±1.03	20.91±0.89
Canopy area (m^2)	489.32±67.29	74.01±7.16	130.11±21.43
Five most surveyed species (in order of decreasing abundance)	*F. religiosa, F. benghalensis, F. rumphii, F. microcarpa, F. benjamina*	*Artocarpus heterophyllus, Tectona grandis, Artocarpus lakoocha, Syzgium cumini, Toona ciliata*	*Syzgium cumini* (non-fruiting), *Albizia lucidor, Albizia procera, Mangifera indica* (non-fruiting), *Neolamarckia cadamba*

Table 2 Model selection results for a set of the most parsimonious generalized linear models (quasi-Poisson family), modelling the (a) abundance and (b) richness of insectivorous birds in 102 isolated trees, in Assam. The predictor variables included the land use surrounding the trees, tree type, tree size, the distance to the nearest protected area with intact forest (Dist1) and the distance to any forest (Dist2). An interaction between tree type and tree size (Int.) was also included as a term in the model selection as a fixed term. The best model (i.e. lowest $QAIC_c$) and all models within $\Delta QAIC_c$ of < 2 of the best model are given for both (a) and (b). The weight of evidence of each variable, calculated by summing the quasi-Akaike weights of all the models in which a variable was included is also given. + indicates a significant effect of a categorical variable. A blank space indicates that a variable was not included in a model. (L) indicates predictor variables that were log transformed. The $\Delta QAIC_c$ ($\Delta QAIC_c$) and $QAIC_c$ weights ($wQAIC_c$) for each model selection are also presented. *these variables were fixed in the model selection procedure and thus the WoE values are constrained.

a) Abundance

Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	$\Delta QAIC_c$	$wQAIC_c$
1		+	0.39	0.33		+	0	0.38
2		+	0.36			+	0.9	0.24
Weight of evidence	0.18	1*	1*	0.59	0.23	1*		

b) Richness

Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	$\Delta QAIC_c$	$wQAIC_c$
1		+	0.32			+	0	0.39
2		+	0.34	0.13		+	1.83	0.16
3	+	+	0.17			+	1.84	0.16
Weight of evidence	0.27	1*	1*	0.28	0.24	1*		

Table 3 Model selection results for a set of the most parsimonious linear models, modelling the functional dispersion of insectivorous birds in 102 isolated trees, in Assam. The predictor variables included the land use surrounding the trees, tree type, tree size, the distance to the nearest protected area with intact forest (Dist1) and the distance to any forest (Dist2). An interaction between tree type and tree size (Int.) was also included as a term in the model selection as a fixed term. The best model (i.e. lowest AIC_c) and all models within ΔAIC_c of < 2 of the best model are given. The weight of evidence of each variable, calculated by summing the Akaike weights of all the models in which a variable was included, and a bootstrapped baseline (see Materials and methods) with which to compare these values to are also given. + indicates a significant effect of a categorical variable. A blank space indicates that a variable was not included in a model. (L) indicates predictor variables that were log transformed. The ΔAIC_c (ΔAIC_c) and AIC_c weights ($wAIC_c$) for each model selection are also presented. *these variables were fixed in the model selection procedure and thus the WoE values are constrained.

Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	ΔAIC_c	$wAIC_c$
1	+	+	-0.06			+	0	0.5
Weight of evidence	0.87	1*	1*	0.26	0.24	1*		
Weight of evidence baseline	0.16	0.23	0.36	0.29	0.29	NA		

Figure legends

Figure 1: A map highlighting the study site location. The inlay shows India and the location of the study landscape within Assam.

Figure 2: The functional dendrogram converted into a tree object, for 33 insectivorous bird species sampled in isolated trees in Assam, India. The dendrogram was constructed by first transforming the species – trait data into a distance matrix (Euclidean distance), and then using the UPGMA clustering algorithm.

Figure 3: Mean insectivore abundance, richness, and FDis (functional dispersion) recorded in isolated tree assemblages in Golaghat District, Assam, India. For *Ficus* trees: n=40; fruit: n=33; and large: n=31. Error bars are standard error.

Figure 4: The relationship between tree size and insectivorous bird species richness for 104 isolated trees in Assam. The data have been split according to the three tree types analysed in the study: fig trees (type 1; red line), non-fig fruiting trees (type 2; green line) and non-fruiting trees (type 3; blue line). The tree size data have been scaled in order for each tree type to cover the same range of tree size; this was achieved by first adding a constant (1.5) to each tree size value (PCA axis; see Methods and material) and then dividing each tree size value by the maximum tree size within that tree type. As the data are not normally distributed we simply fitted loess best fit lines for each of the three tree types, in order to get a rough idea of the patterns.

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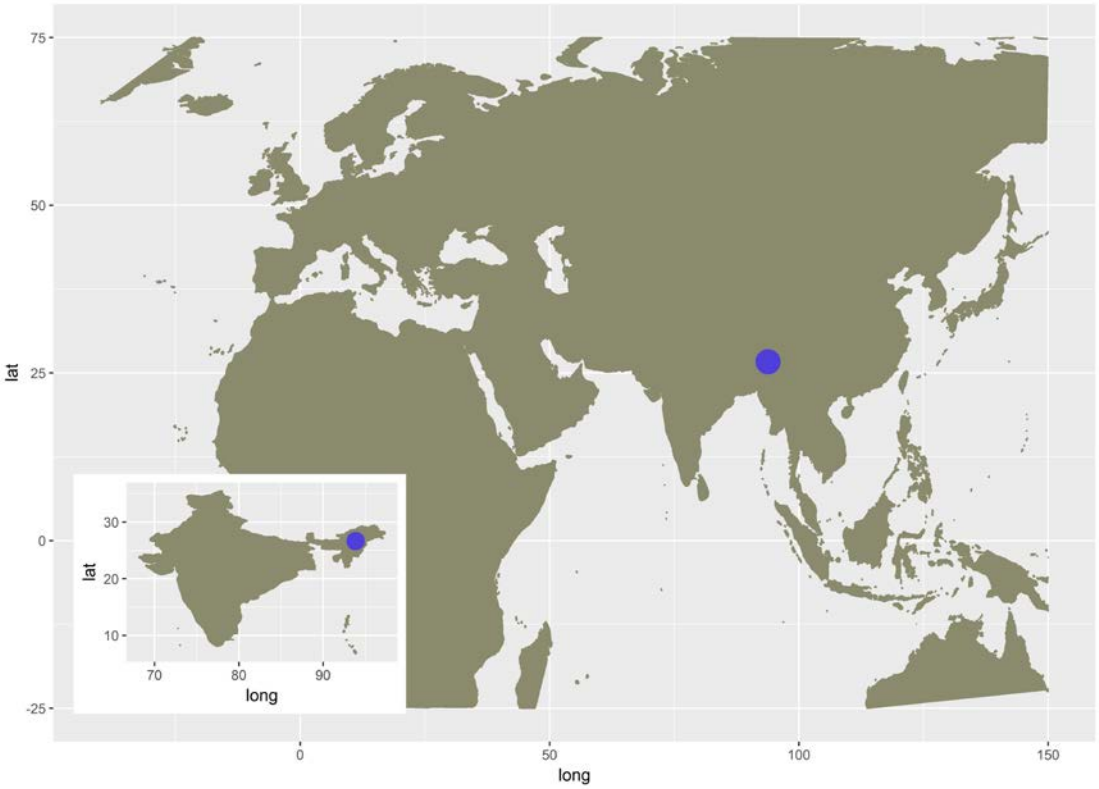

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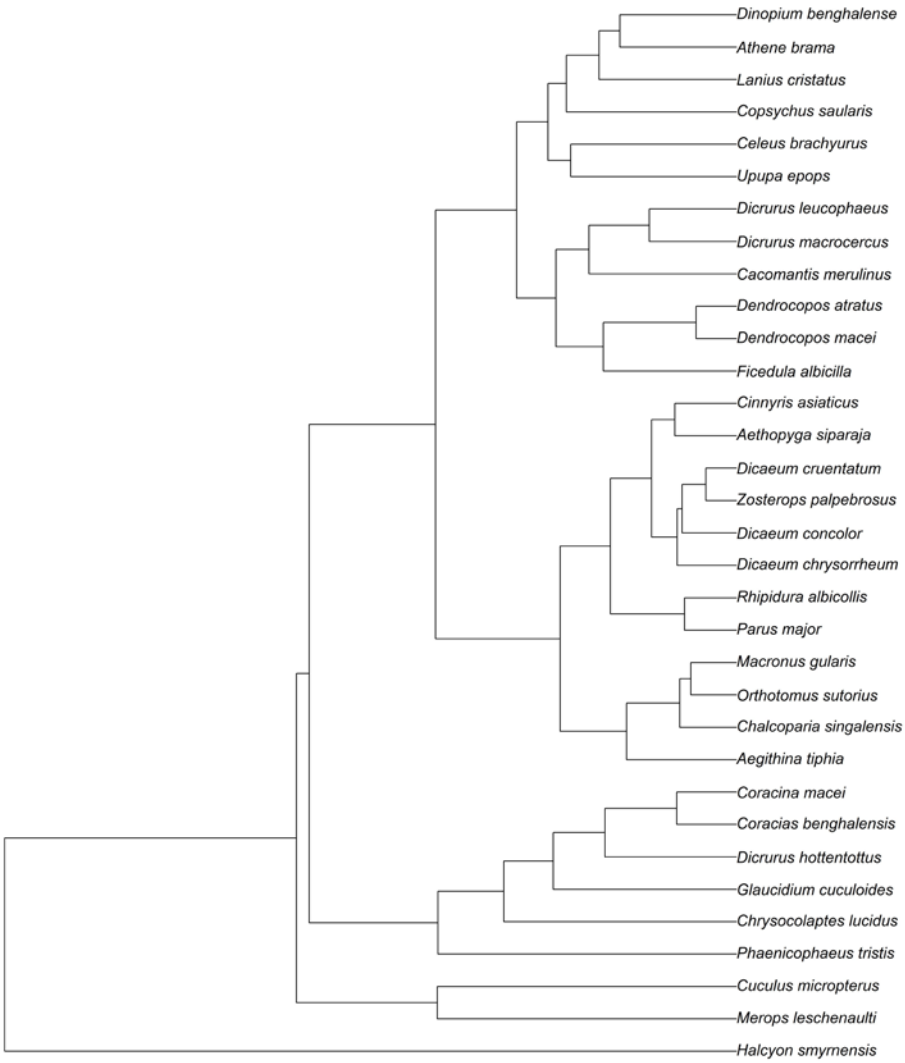
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Athene brama
Lanius cristatus
Copsychus saularis
Celeus brachyurus
Upupa epops
Dicrurus leucophaeus
Dicrurus macrocercus
Cacomantis merulinus
Dendrocopos atratus
Dendrocopos macei
Ficedula albicilla
Cinnyris asiaticus
Aethopyga siparaja
Dicaeum cruentatum
Zosterops palpebrosus
Dicaeum concolor
Dicaeum chrysorrheum
Rhipidura albicollis
Parus major
Macronus gularis
Orthotomus sutorius
Chalcoparia singalensis
Aegithina tiphia
Coracina macei
Coracias benghalensis
Dicrurus hottentottus
Glaucidium cuculoides
Chrysocolaptes lucidus
Phaenicophaeus tristis
Cuculus micropterus
Merops leschenaulti
Halcyon smyrnensis

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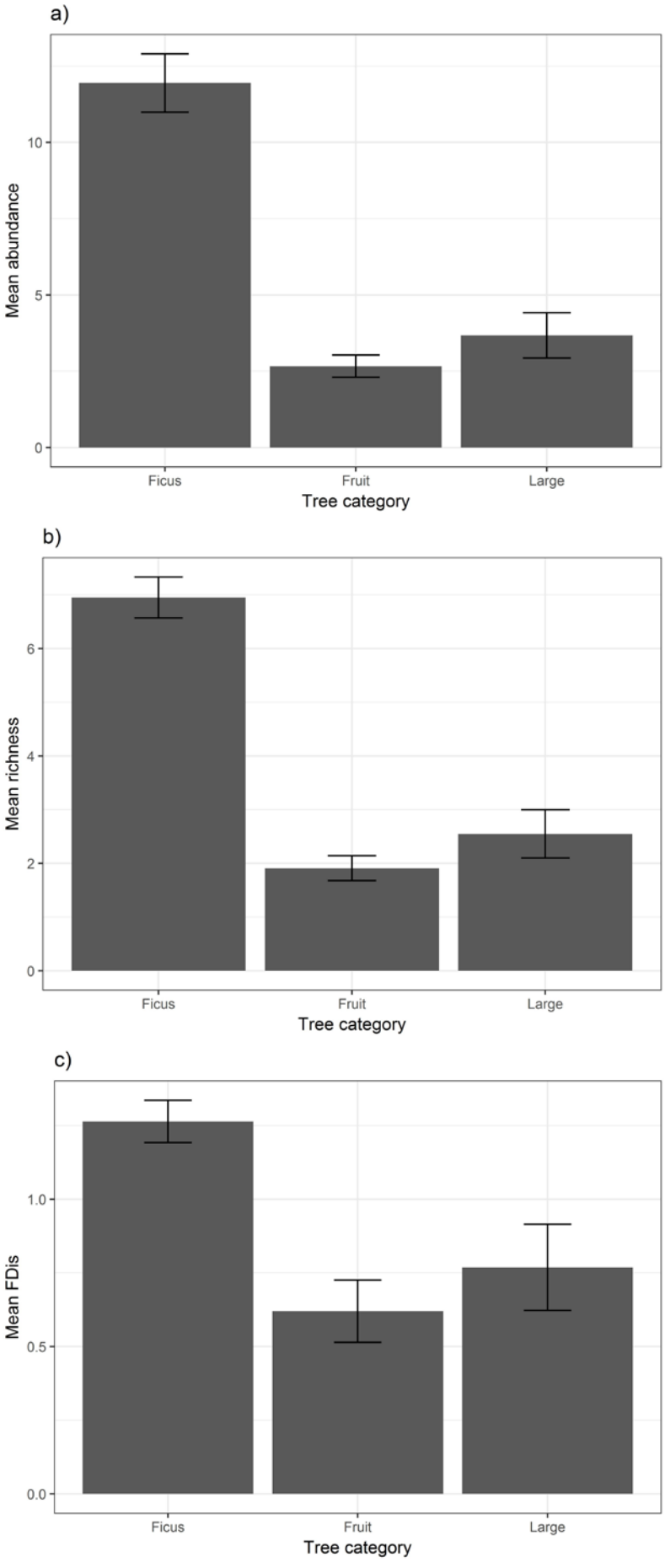
a)
Mean abundance
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b)
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c)
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Fruit
Large
Tree category

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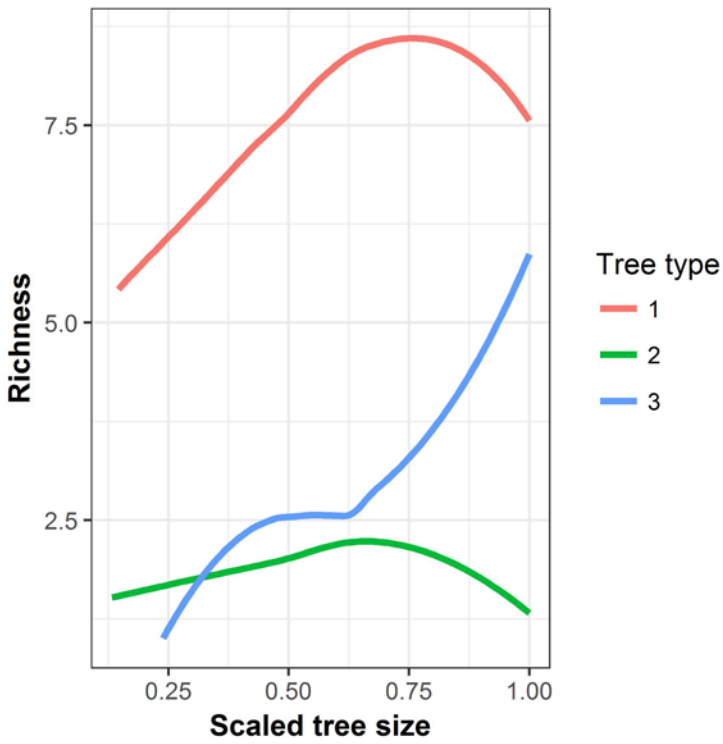

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Assessing the relative importance of isolated *Ficus* trees to insectivorous birds in an Indian human-modified tropical landscape – Supporting information

Biodiversity and Conservation

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Supporting information 1:

To calculate the area of land under agricultural production in the world's tropics, we followed the methodology of Phalan et al. 2013. We defined tropical countries as those that have at least one-third of their land area between the Tropics of Cancer and Capricorn, producing a list of 129 countries. We downloaded data on the extent of total agricultural area in each of these countries from FAO STAT (2014) for the most recent year (2011). We summed these figures to produce an estimate of the total land area under agricultural production in tropical countries (2,455,649,900 ha, rounded to 2.5 billion ha).

Supporting information 2:

To compute functional diversity scores, we first collected ecomorphological trait data on the 34 insectivore species recorded in the study. We measured traits associated with locomotive behaviour (tarsus length, wing chord, and tail length), dispersal

ability (Kipp's distance, hand-wing index), gape size (gape width), bill structure (culmen length, bull length from nares, bill width, bill depth), and body size (via a Principal Components Analysis, PCA).

Specifically, we measured four specimens of the local population for each species recorded. In almost all cases we were able to measure specimens collected within 150 km of the study area. Two adult males and two adult females of each species were measured with 150 mm outside diameter dial callipers (accurate to 0.1 mm), wing rulers, and tail rulers (accurate to 0.5 mm). The measurements taken were: culmen length (from the base of the skull to the tip of the bill), bill length from nares (from the anterior edge of the nares to the tip of the bill), bill width (the width of the bill at the anterior of the nares), bill depth (the depth of the bill at the anterior of the nares), gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation to the base of the toes, where the scalation pattern changes), wing chord (from the bend in the wing to the unflattened longest primary), Kipp's distance (the distance from the longest primary to the first secondary), and tail length (to the tip of the longest retrix).

As weight data for birds are often variable (Clark 1979), we preferred to measure body size through a PCA. We initially conducted a pair of PCA analyses, one for locomotive ability (with input measurements of tail length, wing chord, and tarsus length) and one for bill shape (with bill depth, width, and length from nares) using oblique rotation with Kaiser stopping criterion extraction (eigenvalues >1). Each of these PCAs produced two components. In both cases, the first related to size, while the second components were taken as indices for locomotive ability and bill shape, respectively. To produce one index for body size, we ran an additional PCA using the first components from the original analyses (Trisos et al. *in press*). To create an index

for dispersal ability that standardizes for bird size, we calculated the hand-wing index (Claramunt et al. 2012), which is a surrogate for flight performance, migratory behaviour, and natal dispersion in birds.

Supporting information 3:

We used Laliberté and Legendre's functional dispersion (FDis) index to measure functional diversity in our dataset (Laliberté & Legendre 2010). This represents the spread of the species in quantitative trait space by calculating a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre 2010). A major advantage of FDis over other measures, such as FRic, FEve, and FDiv (Villéger et al. 2008; Mouchet et al. 2010) is that it can be calculated for communities composed of only two species, rather than a minimum of three, which was important for the species-poor insectivore assemblages in the isolated trees. It is also independent of species richness, and can be weighted by abundance, both of which were important considerations for our study.

Supporting information 4:

Table S1: Parameter estimates and standard errors for all terms within the best model, modelling the abundance of insectivorous birds in 102 isolated trees, in Assam. The best model was selected based on comparing $QAIC_c$ values of a complete set of models after fixing the interaction term between tree type and tree size. The predictors included in the best model are tree type (a categorical variable with three levels: 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see Materials and methods), distance between the tree and the nearest protected area with intact forest (Distance), tree size (the first axis of a PCA using three tree size variables; measured on a log scale) and an interaction between tree size and tree type.

Model term	Estimate	Std. error
Intercept	1.20	0.58
Distance	0.33	0.19
Tree type 2	-0.48	0.47
Tree type 3	-0.20	0.45
Tree size	0.39	0.14
Tree type 2 * tree size	-0.37	0.35
Tree type 3 * tree size	0.75	0.39

Table S2: Parameter estimates and standard errors for all terms within the best model, modelling the richness of insectivorous birds in 102 isolated trees, in Assam. The best model was selected based on comparing $QAIC_c$ values of a complete set of models after fixing the interaction term between tree type and tree size. The predictors included in the best model are tree type (a categorical variable with three levels: 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see Materials and methods), tree size (the first axis of a PCA using three tree size variables; measured on a log scale) and an interaction between tree size and tree type.

Model term	Estimate	Std. error
Intercept	1.72	0.12
Tree type 2	-1.00	0.21
Tree type 3	-0.79	0.17
Tree size	0.32	0.14
Tree type 2 * tree size	-0.13	0.32

Tree type 3 * tree size	0.65	0.35

Table S3: Parameter estimates and standard errors for all terms within the best model, modelling the functional dispersion of insectivorous birds in 102 isolated trees, in Assam. The best model was selected based on comparing AIC_c values of a complete set of models after fixing the interaction term between tree type and tree size. The predictors included in the best model are land use (on an ordinal scale: 1=low, 2=medium and 3=high land use intensity), tree type (a categorical variable with three levels: 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see Materials and methods), tree size (the first axis of a PCA using three tree size variables; measured on a log scale) and an interaction between tree size and tree type.

Model term	Estimate	Std. error
Intercept	1.17	0.49
Land use 2	-0.64	0.34
Land use 3	-1.18	0.41
Tree type 2	-1.43	0.38
Tree type 3	-1.27	0.38
Tree size	-0.06	0.36
Tree type 2 * tree size	0.08	0.49
Tree type 3 * tree size	1.42	0.6

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